A NEW SPECIES OF *CYMATIOSPHAERA* (ACRITARCHA) WITH CONSTANT FIELD TABULATION FROM THE DEVONIAN OF TENNESSEE

by A. B. REAUGH

ABSTRACT. The acritarch *Cymatiosphaera peifferi* sp. nov. from the Devonian Chattanooga shales in north-eastern Tennessee, U.S.A., has a characteristic arrangement of polygonal areas, or fields, on the central body. Two distinct kinds of fields, polar and subequatorial, differ in form and symmetry. Fields are arranged according to a constant tabulation pattern (1:5:5:1) with pentagonal symmetry developed around the polar field on each hemisphere.

SPECIES of the acritarch genus *Cymatiosphaera* are generally described in terms of central body diameter, membrane height, and the number and width of fields on the central body. In addition to these characteristics, the arrangement of fields on the central body is proposed here as a means for distinguishing some species within the genus. Description of fields is based on geometric shape and symmetry, and the arrangement of fields provides an additional parameter for identification of form taxa. When general aspects and dimensions are similar (as they are for many *Cymatiosphaera* species), characteristic differences in the arrangement of fields on the central body can be used to separate taxa which would otherwise be indistinguishable.

Specimens of the new taxon described here have a constant tabulation pattern as well as minor differences in wall ultrasculpture and in details of the junction of the membranes with the central body.

STRATIGRAPHY AND AGE

The material was examined as part of a detailed palynologic investigation of the Devonian–Mississippian black shales in north-eastern Tennessee. Specimens were recovered by standard palynologic techniques from samples of the lower part of a thick section of black shales outcropping in Poor Valley and on the dip slope of Clinch Mountain in Hawkins County (Dennison and Boucot 1974). Samples were collected at 1·5 metre (five feet) intervals in roadcuts along Tennessee Route 70 (from 782,550′ N., and 2,876,720′ E. to 779,620′ N. and 2,874,220′ E. Tennessee Grid Coordinates as read from TVA-USGS maps). These palynomorphs represent less than 1% of all palynomorphs in assemblages which include spores, *Tasmanites*, leiospheres, and other acritarchs. Text-fig. 1 shows the range of all specimens and the different ranges of the two kinds of ultrasculpture.

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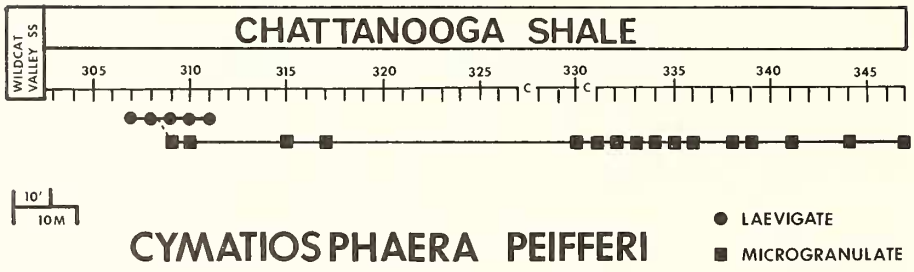


TEXT-FIG. 1. Stratigraphic range of *Cymatiosphaera peifferi* showing ranges of laevigate and microgranulate forms. The species is found in the lower part of the Chattanooga Shale above the Lower Devonian Wildcat Valley Sandstone. The 'c's designate covered intervals much greater than five feet.

Acritarchs associated with the new taxon are also found in the Devonian of the Algerian Sahara (Jardine *et al.* 1974, pp. 105–107). They support a Couvinian–Givetian age (palynologic zones L_2-L_3) based on the joint presence of *Navifusa bacillum*, *Stellinium octoaster*, *Polyedryxium decorum*, *Daillidium quadridactylites*, and *Duvernaysphaera tessela* in samples 307 to 311.

TERMINOLOGY

Cymatiosphaera species have been catalogued by Eisenack *et al.* (1973, pp. 243–367). The terminology describing morphology in *Cymatiosphaera* spp. varies from author to author. Surfaces are divided into polygonal areas variously termed polygonal fields (Downie 1959; Deflandre and Cookson 1955; Wicander 1974; Deunff 1961 as 'champs polygonaux'), polygonal areas (Cramer 1964; Davey 1970; Slavikova 1968), segments (Staplin 1961), or campi (Cramer and Diez 1972). Structures delimiting the polygonal areas on the central body are called membranes (Deflandre and Cookson 1955; Wall 1965; Deunff 1961; Slavikova 1968), muri (Cramer and Diez 1972), partitions (Downie 1959), crests (Cramer 1964), or ridges (Wicander 1974; Davey 1970; Staplin 1961).

The terms fields and membranes are used here to describe the polygonal areas on the surface of the central bodies and the thin walled structures normal to the central body which delimit the fields.

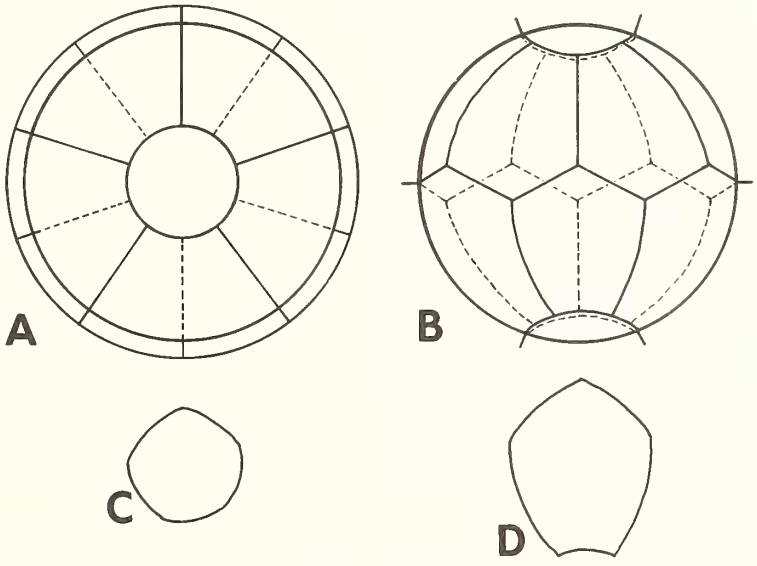
Rasul (1974, p. 43) used the term tabulation to apply to the number and arrangement of the polygonal areas on the Tremadoc acritarch *Cymatiogalea*, analogous to the use of this term in describing dinoflagellates. The term tabulation is here applied to the genus *Cymatiosphaera* and defines the number and arrangement of fields. Although the field pattern resembles that of *Cymatiogalea*, there is no evidence for excystment through an operculate pylome as in that genus.

TABULATION

A geometric arrangement of fields on *Cymatiosphaera* specimens has been indirectly reported for several Devonian species. Membranes of *C. cubus* Deunff, 1961 and *C. carminae* Cramer, 1964 correspond to the edges of a cube. Illustrated specimens have six fields of equal form and size arranged in groups of three fields around triad axes of symmetry at the corners. All specimens presumably have symmetry elements inherent in a cube. Staplin (1961) reported a more complex arrangement of five fields around opposite end fields in *C. pentaster* Staplin, 1961.

For other *Cymatiosphaera* species the range in number of fields is included in the species description, but geometric definitions of fields on the central body are not given. Fields are said to be polygonal, but relationships of the fields to one another are neither defined nor illustrated *per se*. Comparisons of specimens of the same size, membrane height, and field diameters may neglect the geometric forms on the surface of the central body. The arrangement of the fields and their shapes will be shown in this paper to be constant in specimens within the new species and a characteristic useful for differentiating taxa of similar general aspect.

Specimens of the new *Cymatiosphaera* species have the same constant arrangement of two kinds of fields, polar fields and subequatorial fields. Polar fields (text-fig. 2C) are rounded or pentagonal, with radial or pentagonal symmetry. Subequatorial fields (text-fig. 2D) are bilaterally symmetrical, pentagonal fields that are arranged around the equator of the palynomorph (text-fig. 2B). A polar view of the holotype of *C. peifferi* sp. nov. (Pl. 95, figs. 1, 2) shows the relationship of the polar and subequatorial fields (idealized in text-fig. 2A).



TEXT-FIG. 2. Schematic diagram of *Cymatiosphaera peifferi* showing arrangement of fields. A, polar view with central polar field surrounded by five subequatorial fields. Comparable fields on the lower hemisphere are shown by dashed lines. B, equatorial view showing zigzag line at the juncture of the subequatorial fields along the equator. C, individual polar field. D, individual subequatorial field.

The precise shape of the polar field is uncertain. It is in direct contact with five equidimensional edges of the five subequatorial fields. Secondary folds caused by compression commonly occur along the boundary (Pl. 95, fig. 3, drawn in text-fig. 3A) and exaggerate the contact so that a polar field, whose shape logically would be pentagonal, appears to be round.

The polar field is surrounded by five subequatorial fields on the upper hemisphere; on the lower hemisphere the same pattern is mirrored with 36° offset at the equator. There is no difference in fields on the two hemispheres, and, thus, there is no distinction between the two hemispheres. The offset at the equator results in a zigzag membrane around the equator. The axis of bilateral symmetry of each subequatorial field is normal to the equator which the zigzag line repeatedly intersects.

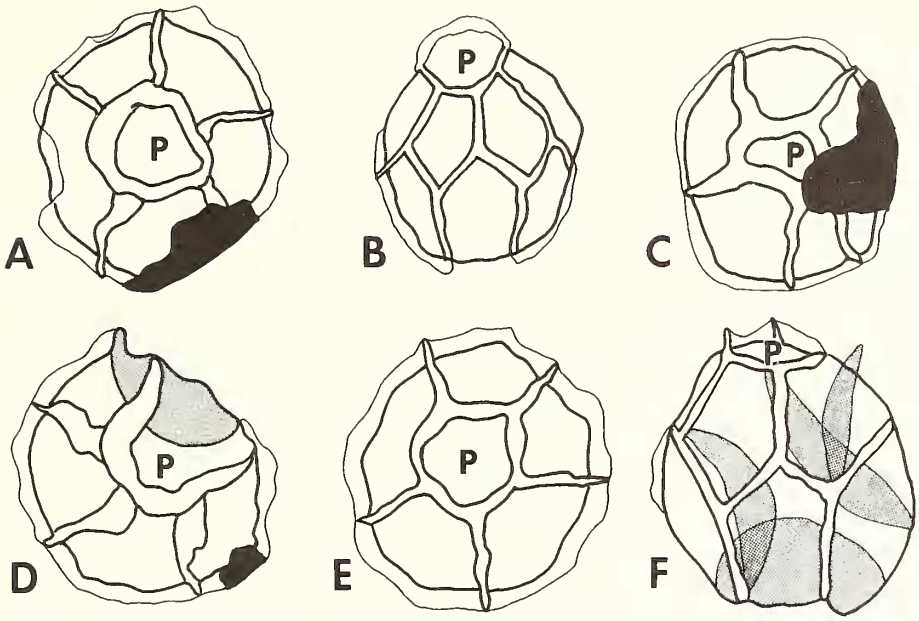
The tabulation pattern of this taxon is 1:5:5:1, where the first and last numbers refer to polar fields and the middle numbers to subequatorial fields. The terms pre-equatorial and post-equatorial (as used with *Cymatiogalea* specimens) cannot be applied in the absence of criteria for such distinctions. Specimens lacking polar or equatorial orientation and with secondary folds may be recognized as belonging to the taxon by location of the zigzag line and a check for bilateral symmetry on the adjacent fields.

Text-figs. 3B–F are interpretations of specimens illustrated on Pl. 95. Although tabulation patterns are not immediately obvious from the photographs, the line drawings show the distinctions between folds and membranes and lead to distinction of the polar fields and surrounding subequatorial fields. From such sketches, tabulation patterns for all the specimens in a population can be deduced.

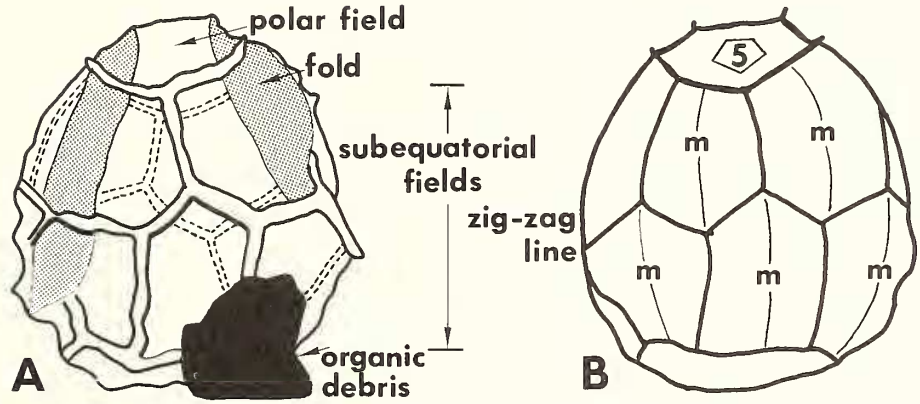
Although the field tabulation pattern for the new species is constant among specimens of the same species, it differs markedly from the pattern of another Devonian taxon.

COMPARISON WITH A SIMILAR TAXON

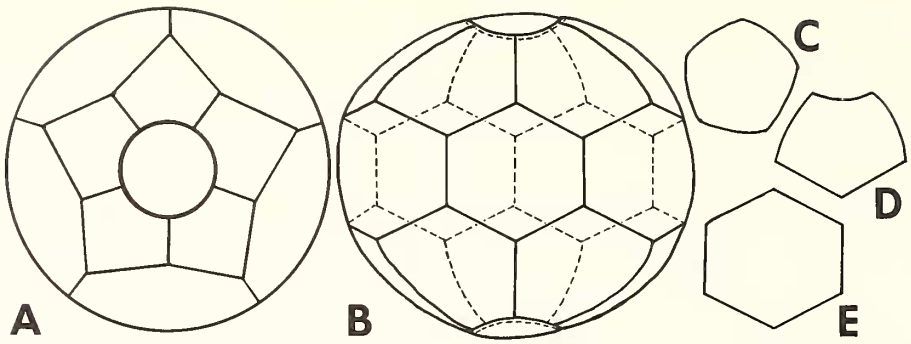
Although slightly smaller, ?*Polyedryxium mirum* Deunff, 1957 has a holotype (Deunff 1971, pl. 4, figs. 16, 16*a*) somewhat similar to the new taxon in details of membrane height, field number, and general field form. There are, however, differences between the fields of ?*P. mirum* and *Cymatiosphaera peifferi*. Text-figs. 5A, B show a field arrangement for ?*P. mirum* based on the illustration of the holotype (Deunff 1971). Although marginal folds are indistinct on the equatorial view, there are apparently three different field types: polar fields (text-fig. 5C), subequatorial fields (text-fig. 5D), and equatorial fields (text-fig. 5E). Subequatorial and equatorial fields are clearly illustrated on the photograph of the holotype. Each polar field is apparently an equal-sided pentagon because of its location between five equidimensional edges of the subequatorial fields. If symmetry around a polar field is assumed (only radial or cubic symmetry has been found in a review of Devonian forms illustrated in Eisenack *et al.* 1973), the total body plan would be a complex arrangement of three field types, each with distinctive symmetry, as shown in polar and equatorial view in text-figs. 5A, B. A tabulation pattern of 1:5:5:5:1 and the distinctive shapes of the fields are distinctive variations from the pattern seen in *C. peifferi*.



TEXT-FIG. 3. Simplified views of illustrated specimens emphasizing field tabulation patterns. Overlying organic debris is shown by solid black areas, folds by stippled patterned areas. Each polar field illustrated is indicated by 'P'. Specimens figured in Pl. 95 are illustrated by the following line drawings: Pl. 95 fig. 3 = A; fig. 4 = B; fig. 7 = C; fig. 8 = D; fig. 9 = E; fig. 12 = F.



TEXT-FIG. 4. Diagrammatic view of specimen illustrated in Pl. 95 figs. 10, 11. A shows field locations as well as secondary folds and overlying organic debris. B shows symmetry elements of the different fields, relative to the position of the fields on the specimen.



TEXT-FIG. 5. Schematic diagram of ?*Polyedryxium mira* (Deunff, 1957) drawn after Deunff 1971, pl. 4, fig. 16, 16*a*. A, hypothetical polar view. B, equatorial view after illustrations by Deunff. C–E, individual fields: C, polar field with radial or pentagonal symmetry; D, subequatorial field with simple bilateral symmetry; E, equatorial field with 2 planes of bilateral symmetry.

In the light of this interpretation of ?*P. mirum*, Dr. Jean Deunff kindly re-examined the type of ?*P. mirum* (LPB 2933) and observed that there are differences among the polygonal fields, and that in particular the equatorial fields have smaller surfaces than do the polar fields on that specimen (Deunff, pers. comm. 1977). He further sees the structure of ?*P. mirum* as more complex than that of *C. peifferi* in the equatorial region.

COMPARISONS WITH OTHER GENERA

Other taxa have similar tabulation patterns dictated by the arrangement and shape of the polygonal areas on the central bodies. The genus *Cymatiogalea* (Deunff) Rasul includes acritarchs whose 'test surface is divided into polygonal areas . . . [which] exhibit some sort of a tabulation pattern, usually observable' (Rasul 1974, p. 52). There are, however, a variety of tabulation patterns associated with individual species of *Cymatiogalea*, reflecting differences in the shapes of the constituent polygonal areas. Any change in the shape of one area would alter the shape and fit of the adjacent areas. Although some areas may be defined by symmetry, others exhibit no symmetry, and in *C. multarea* (Deunff) no areas are symmetrical (Rasul 1974, text-fig. 4). In *C. cristata* the third and fourth areas on the second row may be defined by two normal planes of bilateral symmetry, but the fifth area has no symmetry. Thus it appears that symmetry cannot be used to define *Cymatiogalea* species. In contrast, determination of the symmetry of any three fields adjacent to a triple junction in *Cymatiosphaera peifferi* enables prediction of the location, form, and orientation of the other fields, as was done for all fifty-seven measured specimens.

Tests of the extant alga *Pterosperma nationalis* exhibit variability comparable to that of *Cymatiogalea*, having different shaped polygonal areas: all three-sided, all four-sided, three- and four-sided, and four- or five-sided (Boalch and Parke 1971). There is no comparable variability in the group of *Cymatiosphaera* found with *C. peifferi*. The others are either a different size, have a different membrane height

relative to body width, or have many more fields on the specimens. In younger samples from the same strike belt (Reaugh in prep.) there is a *Cymatiosphaera* species with a microgranulate surface, a similar membrane, and a comparable body size. The sole morphologic difference is the form and arrangement of the fields which are six equidimensional, four-sided fields arranged as are the faces of a cube. Were it found in the same samples as *C. peifferi*, a similarity to *P. nationalis* could be argued with this 'cubic' form representing the 'all four-sided' forms, but the range of the 'cubic' forms is completely disjunct from that of *C. peifferi.*

SYSTEMATIC DESCRIPTION

Genus CYMATIOSPHAERA O. Wetzel, 1933, emend. Deflandre, 1954

Cymatiosphaera peifferi sp. nov.

Plate 95, figs. 1–12; text-figs. 2–4

Description. Spherical to subspherical central body; central body laevigate to microgranulate, granules up to 0·5 μm in diameter. Surface divided into polygonal fields outlined by vertical membranes; specimens are divided into two hemispheres by an equatorial zigzag line formed by the succession of membranes between the subequatorial fields. Each hemisphere has a rounded to pentagonal field at its pole; the polar field is surrounded by five bilaterally symmetrical, pentagonal subequatorial fields which extend from the polar field to slightly beneath the equator on the lower hemisphere. There are twelve fields on a specimen: two polar fields and ten subequatorial fields.

Dimensions. Central body diameter 36–58 μm (mean 45·8 μm, S.D. 6·6); membrane height 2·7–5·4 μm depending on orientation and secondary folding; fifty-seven specimens measured.

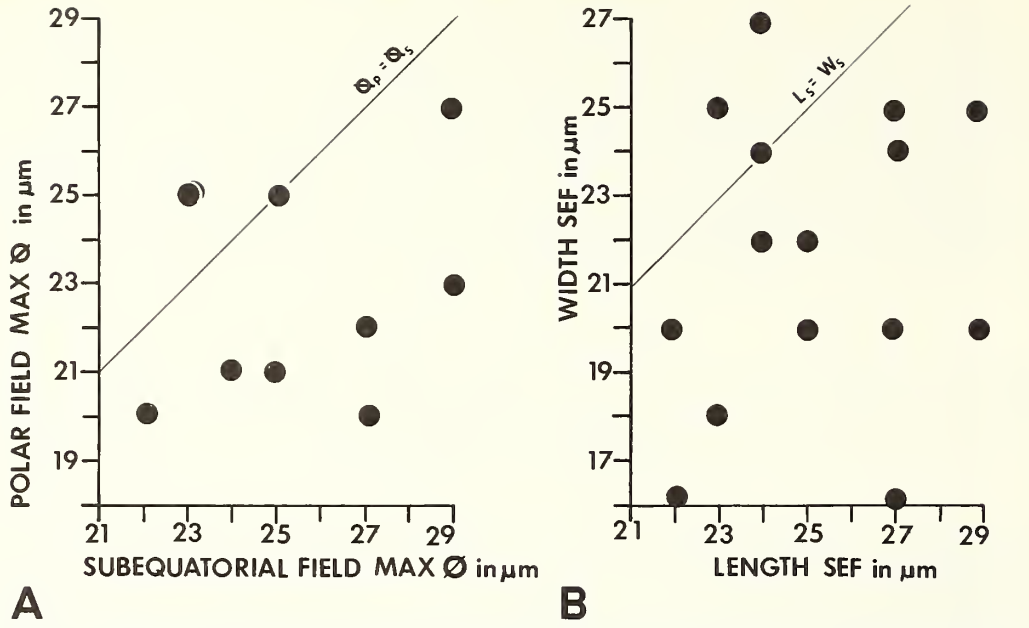
Holotype. Specimen illustrated on Pl. 95, figs. 1, 2, located on slide 307-4 at R 15·7 and +12·8 relative to the north-eastern corner of the slide, and stored in the University of Tennessee, Department of Geological Sciences Palynology Collection, Knoxville, Tennessee, 37916, U.S.A.

Type locality. Chattanooga shales on Tennessee State Route 70 in Hawkins County, Tennessee, on the dip slope of Clinch Mountain.

Geologic age. Givetian–?Frasnian.

Discussion. Specimens assignable to *C. peifferi* may be divided into two groups based on poorly defined surface ultrasculpture. Those with laevigate ultrasculpture (Pl. 95, figs. 1–3) are found lower in the stratigraphic section (text-fig. 1, sample 307–311) than are specimens with a microgranulate surface (Pl. 95, figs. 4–11). The latter are longer ranging (text-fig. 1, samples 309–347) and, in addition, occasionally exhibit a differentiation of the membrane (Pl. 95, fig. 6).

All specimens are compressed, and the accompanying folds obscure the field outlines and make measurement of individual fields difficult. Due to differences in orientation, only a few specimens could be located with both polar and subequatorial fields clearly shown. In those cases where measurements could be obtained without difficulty, the polar fields are slightly smaller than the longest diagonal on adjacent subequatorial fields (text-fig. 6A).



TEXT-FIG. 6. Dimensions of fields of *Cymatiosphaera peifferi*. In A the maximum diameter (Ø) of polar fields is plotted against maximum diameter of adjacent subequatorial fields on the same specimen. B plots two dimensions of individual subequatorial fields (SEF): length (the measurement parallel to the axis of bilateral symmetry and normal to the equator) and width (the longest dimension normal to the length diagonal).

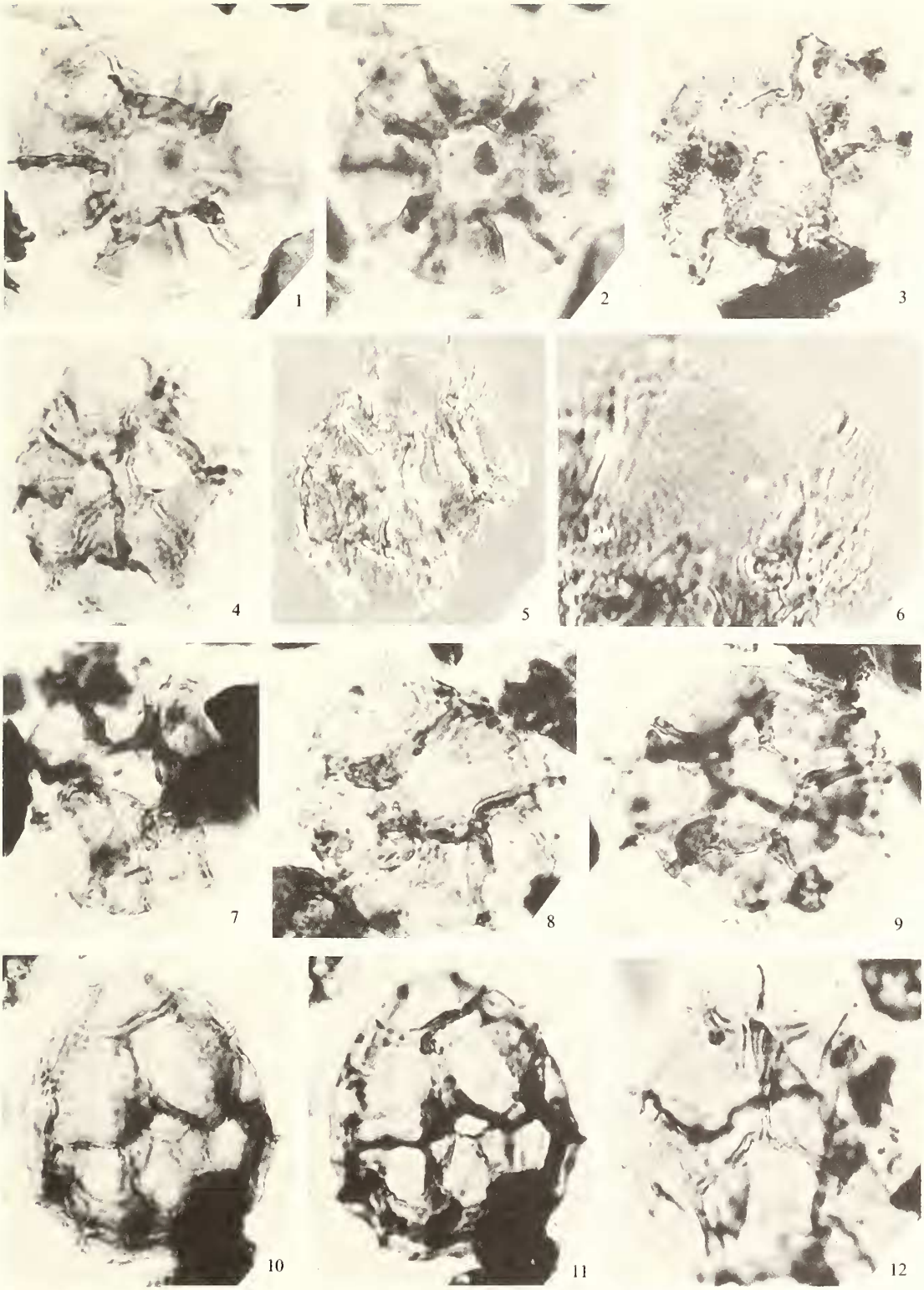
Although it may be difficult to distinguish fields by recognition of the symmetry of individual fields, the zigzag line is often very obvious on equatorially oriented specimens. The subequatorial fields adjacent to the zigzag line are bilaterally symmetrical and are longer on the axis of bilateral symmetry than on any diameter normal to that axis (text-fig. 6B).

C. labyrinthica Wicander is larger and has a different membrane, and *C. parvicarina* Wicander is the same size but has much smaller fields. Neither species has a field arrangement comparable to the new taxon. *C. peifferi* is named for the late

EXPLANATION OF PLATE 95

All specimens are from outcrops of Chattanooga Shale on Route 70 in Poor Valley and on the dip slope of Clinch Mountain, Hawkins County, Tennessee, U.S.A. All figs. ×780 unless otherwise stated.

Figs. 1–12. *Cymatiosphaera peifferi* sp. nov. 1, 2, upper and lower focus of holotype showing the upper and lower polar fields and illustrating the offset of subequatorial fields and the radial symmetry around the polar fields (slide 307-4: R 15.7, +12-8). 3, shows exaggerated folding around the polar field (slide 310-1: R 32.0, +5.2). 4–6, equatorial views of a specimen with microgranulate ultrastructure, and fig. 6 (×1200) also shows the fine differentiation of the membrane into a thin outer layer beyond a thicker basal layer (slide 334-2: R 31.2, +12.7). 7–9, polar views which illustrate the kinds of folding that can obscure field outlines; 7, slide 309-1: R 6.9, +15.7; 8, slide 309-1: R 6.8 +15.6; 9, slide 336-1: R 15.6, +2.5. 10, 11, two foci of equatorial views of a specimen with clearly illustrated subequatorial fields (slide 335-2: R 7.5, +0.3). 12, shows the zigzag equatorial membrane (slide 307-1: R 11.2, +14.7).

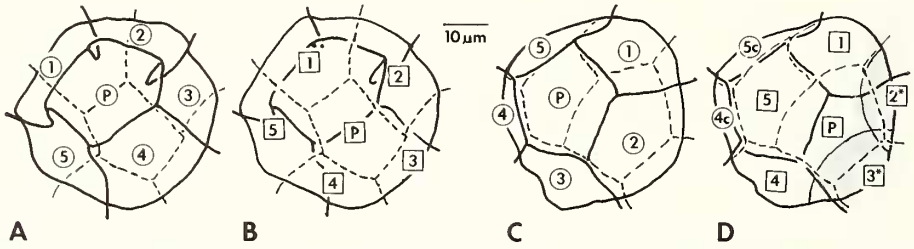


REAUGH, *Cymatiosphaera peifferi* sp. nov.

John S. Peiffer of Culpeper, Virginia, who introduced me to spherical geometry and three-dimensional perception.

Note added in press. Wicander and Loeblich (1977) have recently described *C. ambotrocha* which has a 1:5:5:1 tabulation pattern. Although this pattern is similar to that of *C. peifferi*, the latter is slightly smaller and its holotype has a laevigate surface. Microgranulate forms of *C. peifferi* may represent transitional forms between the two taxa, but those found in the Chattanooga shales do not have the sharply developed granules on the surface of the specimens.

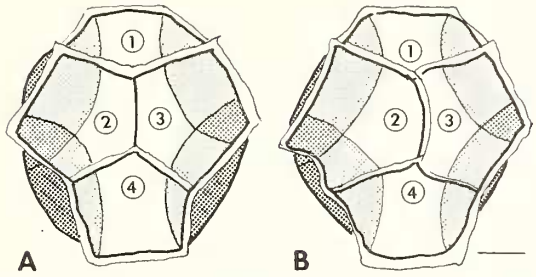
Wicander and Loeblich (1977, p. 136) also described a similar species, *C. antera* on which 'each hemisphere [is] divided into four fields that are separated from each other by a laevigate ridge . . . fields and ridges arranged as an "H", the ends of the "H" being attached to the vesicle wall in such a manner as to pull it up . . . on some specimens one hemisphere may have a central five sided field surrounded by five equal sided fields dividing that hemisphere into 6 instead of four fields'.



TEXT-FIG. 7. Interpretation of *Cymatiosphaera antera* Wicander and Loeblich, 1977 showing 1:5:5:1 tabulation patterns. Field boundaries on the upper hemisphere in focus are shown by solid lines, and the field numbers are circles; field boundaries on the lower hemisphere are shown in dashed lines and the fields in squares. 'P' indicates proposed polar fields, numbered fields are the subequatorial fields. A and B are interpretations of *C. antera* illustrated by Wincander and Loeblich 1977, pl. 1, fig. 7 showing the twelve fields. C and D show *C. antera* of Wicander and Loeblich, pl. 1 fig. 11; fields 4C and 4D are continued from the upper view; fields 2* and 3* are partially visible in regular view, the rest of their area is included in the folded areas.

Of the three specimens illustrated by those authors, two should be assigned in my opinion to *C. ambotrocha* because of their tabulation. Specimen 6156-8:22.7-98.8 (Wicander and Loeblich 1977, pl. 1, fig. 7) 'showing a rare specimen with a central field surrounded by 5 fields' also has six fields on the lower hemisphere according to the interpretation shown here in text-fig. 7A, B. As interpreted, it has a 1:5:5:1 tabulation and should be assigned to *C. ambotrocha*. Figured specimen 6156-6:15.8-96.9 (Wicander and Loeblich 1977, pl. 1, fig. 7) 'showing aspect in near equatorial focus', is interpreted here (text-fig. 7C, D) as being a slightly off-polar view of *C. ambotrocha*.

The holotype of *C. antera* (6157-4:9.4-96.4, Wicander and Loeblich 1977, pl. 1, figs. 10, 12) has clearly illustrated four fields per hemisphere. There is, however, additional vesicle wall material visible, of which there is no mention in the species description. The heavily stippled areas (text-fig. 8A, B of this paper) indicate areas not within



TEXT-FIG. 8. A, B are interpretations of the holotype of *Cymatiosphaera antera* showing the four fields per hemisphere (circled) and the stippled areas representing the areas of vesicle wall not included in those eight fields. A corresponds to pl. 1, fig. 10 of Wicander and Loeblich 1977, and B to their pl. 1, fig. 12.

the four fields per hemisphere. The lighter stipple represents folded regions between the 'four fields per hemisphere'. These areas give evidence that there are more than four fields per hemisphere, and more than eight fields per acritarch. The interpretation shown in text-fig. 8A, B suggests that there are twelve fields on the holotype of *C. antera*. The forms and arrangements of the additional fields are uncertain and geometric comparisons with *C. peifferi* and *C. ambotrocha* cannot be made.

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